

Effect of Temperature and Feeding Preference on Submerged Plants by the Island Apple Snail, *Pomacea insularum* (d'Orbigny, 1839) (Ampullariidae)

L. A. GETTYS, W. T. HALLER, C. R. MUDGE AND T. J. KOSCHNICK

University of Florida Department of Agronomy, Center for Aquatic and Invasive Plants, 7922 NW 71 Street, Gainesville, FL 32653. Tel: 352-846-2516; Fax: 352-392-3462
(e-mail: lgettys@ufl.edu)

Abstract. The island apple snail (*Pomacea insularum* (d'Orbigny, 1839)) is a South American snail that became naturalized in Florida waterways in the mid-1970s and has recently spread throughout much of the state. Food consumption by this herbivorous snail was determined in 10-day feeding trials at temperatures of 15 to 35°C. Optimum feeding of the exotic submerged plant *Hydrilla verticillata* (L.f.) Royle (hydrilla) occurred over a wide temperature range (20 to 35°C). However, snail growth was greatest at temperatures of 20 to 30°C. Free choice plant preference studies were conducted to determine feeding preferences for native and exotic submerged plants. One exotic and two native species (*H. verticillata*, *Najas guadalupensis* (Spreng.) Magnus (southern naiad) and *Chara* sp. (stonewort), respectively) were highly preferred by island apple snails, followed by the two native species *Potamogeton illinoensis* Morong. (Illinois pondweed) and *Vallisneria americana* Michx. (tapegrass). Leaves of the exotic species *Myriophyllum aquaticum* (Vell.) Verdc. (parrotsfeather) were eaten after the more preferred plants were consumed and no significant feeding was noted on the exotic species *Egeria densa* Planch. (Brazilian elodea). While island apple snails have distinct preferences for certain submerged plants, they consumed both native and exotic species, which may significantly affect growth of certain species and will likely change species composition of submerged plant communities in Florida wherever they are common.

Key Words: *canaliculata* complex, feeding preference, Florida waterways, invasive species, temperature effect.

INTRODUCTION

The island apple snail (*Pomacea insularum* (d'Orbigny, 1839)) is native to South and Central America and was most likely introduced into Florida through the aquarium trade (Thompson, 1997). Collections of this exotic snail have been reported sporadically in natural areas of Florida since 1978 (FLMNH, 2007), but recent reports suggest that the species has greatly expanded its range and has invaded virtually all counties in central and southern Florida (Denson, 2005). Specimens of *P. insularum* have been collected from a variety of habitats in Florida, including natural and constructed wetlands, streams, ponds, lakes and ditches that are inundated for most or all of the year. These habitats have earthen bottoms and are characterized by the presence of submerged, floating and/or emergent aquatic macrophytes. Areas frequented by *P. insularum* also typically have structures above the water line (e.g., emergent aquatic plants or man-made structures such as dikes or locks) onto which *P. insularum* deposits eggs.

There has been some confusion regarding the taxonomy of South American apple snails in Florida, but recent DNA studies indicated that the snails present in Florida (originally identified as *P. canaliculata* (Lamarck, 1822)) are actually *P. insularum*

(Rawlings et al., 2007). Field identification of species within the family *Pomacea* is challenging, since external characters are highly plastic and influenced by environmental factors. This is especially true of *P. haustorium* (Reeve, 1856) (titan), *P. canaliculata* (channeled) and *P. insularum* (island) apple snails, which are virtually indistinguishable from one another in morphology and behavior. In fact, these snails are so similar they are often grouped together into a “*canaliculata* complex.” Cazzaniga (2002) stated that all *canaliculata*-like apple snails may constitute a single, highly variable species and further noted that any *canaliculata*-like apple snail has the potential to become a pest and cause damage to aquatic ecosystems. *Canaliculata*-like apple snails can become quite large, but *P. insularum* is considered the largest of the group and can attain a shell height of up to 150 mm (Benson, 2008; Gettys and Haller, 2007).

One factor that influences the feeding of *canaliculata*-like apple snails is temperature. Estebenet and Cazzaniga (1992) and Estebenet and Martin (2002) found that *P. canaliculata* grew most quickly under warm conditions (>25°C) and stopped feeding during cool temperatures (e.g., <18°C). These results suggest that the warm year-round temperatures found throughout much of Florida may provide an ideal habitat for *P. insularum*; therefore, the first objective of this experi-

ment was to measure the effect of temperature on consumption of *Hydrilla verticillata* (L.f.) Royle (hydrilla), an aquatic weed that is ubiquitous in aquatic systems throughout Florida, Texas and other regions that have been invaded by *P. insularum*.

Canaliculata-like snails in the genus *Pomacea* are voracious herbivores and have been introduced to some parts of the world as biocontrol measures to manage aquatic weeds (Cowie, 2002; Okuma et al., 1994; Wada, 1997). Some workers have reported that *canaliculata*-like apple snails actively select their food and exhibit a preference for some plant material. For example, Fukushima et al. (2001) found that *P. canaliculata* preferred most fruits and vegetables to rice seedlings. Lach et al. (2000) stated that *P. canaliculata* selected *Vigna marina* (Burm.) Merr. (beach pea or notched cowpea) over *Eichhornia crassipes* (Mart.) Solms (waterhyacinth), *Ludwigia octovalvis* (Jacq.) P.H. Raven. (primrose willow) and *Pistia stratiotes* L. (water-lettuce). Carlsson and Lacoursiere (2005) stated that *P. canaliculata* virtually eliminated *Lemma minor* L. (duckweed) and *E. crassipes* after 6 and 21 days of grazing, respectively, but reduced the biomass of *Ipomea aquatica* Forsk. (waterspinach) by only 20% after 32 days of grazing. Estebenet (1995) found that *P. canaliculata* preferred *Zannichellia palustris* L. (horned pondweed) over *Myriophyllum elatinoides* Gaudin (water milfoil or Christmas-tree plant) and *Chara contraria* A. Braun ex Kutz. (opposite stonewort); snails had a low preference for *Rorippa nasturtium-aquaticum* [L.] Hayek (watercress) and *Potamogeton striatus* Ruiz & Pavón (broadleaf pondweed) and did not select *Elodea canadensis* LC Rich. in Michx (common waterweed). In contrast, Cazzaniga and Estebenet (1984) and Cowie (2002) suggested that these snails feed indiscriminately on virtually anything, including algae, macrophytes, phytoplankton, detritus and even immature snails of other species. In addition, Peltzer and Lajmanovich (2003) reported that *Hyla pulchella* Duméril & Bibron, 1841 (anuran tadpoles) were consumed by juvenile *P. canaliculata*. A variety of submerged macrophytes species are found in Florida; some species are native, while others are exotic and invasive. Common native aquatic macrophytes in Florida include *Vallisneria americana* Michx. (tape-grass), *Najas guadalupensis* (Spreng.) Magnus (southern naiad), *Potamogeton illinoensis* Morong. (Illinois pondweed), and *Chara* sp. (stonewort). Invasive exotic species common in Florida waters include *H. verticillata* (native to Asia, Africa and Australia), along with the South American natives *Egeria densa* Planch. (Brazilian elodea) and *Myriophyllum aquaticum* (Vell.) Verdc. (parrotsfeather). Native species of macrophytes are more desirable than exotic species, but many aquatic fauna that rely on submerged vegetation as a habitat for nesting and spawning do not discriminate

between native and exotic species. If the *canaliculata*-like *P. insularum* indiscriminately consumes all flora, the consequences to Florida's ecosystem could be devastating since the snail can cause significant changes to wetland ecosystems through herbivory of aquatic macrophytes. High densities of *P. canaliculata* in natural wetlands in Thailand caused an almost complete loss of aquatic macrophytes through grazing (Carlsson et al., 2004). Wetlands in central and south Florida persist under the same environmental conditions as those in Thailand, so it is reasonable to expect the same situation to occur if waterways in Florida become infested with *P. insularum*. Data regarding the feeding habits and macrophyte preferences of *canaliculata*-like apple snails are conflicting and there are no reports that address the feeding habits of snails positively identified as *P. insularum*; therefore, the second objective of this study was to determine if *P. insularum* is truly a non-specific feeder or if the snail shows a feeding preference when presented with a diversity of native and exotic submerged macrophytes commonly found in Florida waterways.

MATERIALS AND METHODS

Several hundred specimens of *P. insularum* were collected from a heavily infested earthen irrigation pond (surface area 0.12 ha; maximum depth 1 m) at a wholesale aquatic plant nursery in Lake City, Florida. Snails were maintained in a covered greenhouse (ambient temperature $28 \pm 3^\circ\text{C}$) at the University of Florida's Center for Aquatic and Invasive Plants in Gainesville, FL for 2 to 3 weeks prior to their utilization in these experiments. Each snail was measured (height and width), weighed and assigned a letter/number combination code using the following system. Snails were assigned one of six letter classes based on weight (A: <25 g; B: 25 to 35 g; C: 35.1 to 45 g; D: 45.1 to 55 g; E: 55.1 to 65 g; and F: >75 g) and were numbered in ascending order (e.g., snail D6 weighed between 45.1 and 55 g and was the 6th snail labeled in weight class D). The shell of each snail was gently cleaned and dried using a disposable paper towel, then the alphanumeric code was painted onto the snail shell using nail polish so that snails could easily be identified. This coding system allowed positive identification of each snail and was used to ensure that each snail was only used in a single study.

Effect of Temperature on Consumption

The objective of this study was to measure the effect of temperature on consumption of macrophytes by *P. insularum*. The macrophyte *H. verticillata* was used in this study because it is an exotic species that is ubiquitous in aquatic systems throughout Florida,

Texas and other regions that have been invaded by *P. insularium*. The temperature regimes in this study were chosen to represent the range of seasonal variation in water temperature in Florida. Consumption of *H. verticillata* under five temperature regimes (15°C, 20°C, 25°C, 30°C and 35°C) was investigated in growth chambers (Percival model E36L, Perry, IA). Digital controls on the chambers were programmed to maintain a daylength of 14 hr and to hold water temperature at the target temperature $\pm 0.5^\circ\text{C}$. Four 5-gallon aquaria were placed in each growth chamber. Water was maintained at a depth of ca. 25 cm to provide a water volume of ca. 12 L and aeration was supplied by a standard aquarium aerator. Snails were selected for uniform weight and one snail was placed in each filled aquarium within the growth chamber. Water temperature was adjusted by 3°C per day to reduce shock during the transition from ambient greenhouse temperature ($28 \pm 3^\circ\text{C}$) to the assigned experimental temperature regime. Snails were acclimatized to experimental temperatures for 2, 4 or 6 d for 25°C and 30°C treatments, 20°C and 35°C treatments and 15°C treatment, respectively, and were fed *H. verticillata* ad libitum during acclimatization. Snails were starved for 24 hr after acclimatization and were weighed prior to commencement of each study. Each study lasted 10 d and each snail was offered a total of 90 g of *H. verticillata* during each study (30 g each on days 1, 4 and 7). Water in the aquaria quickly became fouled with feces and detritus, so additional aquaria were filled with water and placed in each growth chamber on days 3 and 6. Snails, aerators and uneaten *H. verticillata* were moved to these clean, acclimatized tanks on days 4 and 7. Total biomass consumption was calculated by weighing uneaten plant material remaining in each aquarium on day 10 of each study and snails were weighed on day 10 as well. Data were analyzed to detect differences in plant biomass consumption and differences in snail weight under each temperature regime.

Feeding Preference

Macrophytes were maintained in a greenhouse under natural daylength during Fall 2005 at the University of Florida's Center for Aquatic and Invasive Plants in Gainesville, FL. All macrophytes were grown in square pots (10 cm square \times 12 cm deep) filled with 1 kg of coarse builder's sand amended with 1 g of Osmocote® Plus 15-8-12 controlled-release fertilizer (The Scotts Co. LLC, Marysville OH). Seven submerged macrophytes – *H. verticillata*, *V. americana*, *E. densa*, *N. guadalupensis*, *P. illinoensis*, *Chara* sp. and *M. aquaticum* – were utilized in this experiment to represent some of the most common native and exotic aquatic species found in Florida waters. Macrophytes were propagated by

vegetative means with either four 10-cm-long apical cuttings per pot (*H. verticillata*, *E. densa*, *N. guadalupensis*, *P. illinoensis* and *M. aquaticum*), one clump of ten 10-cm-long apical cuttings per pot (*Chara* sp.) or three rooted plantlets per pot (*V. americana*). These propagation methods were used because our preliminary studies suggested these protocols would supply snails with sufficient amounts of each macrophyte species. Macrophytes were propagated 7 to 14 d prior to commencement of the experiment and were grown in circular fiberglass tanks (inside diameter 105 cm, water depth 55 cm) filled with well water to a volume of ca. 475 L (pH 8, temperature range ca. 22°C to 32°C).

All food was withheld from snails for 48 hr prior to commencement of the food preference experiments. Naylor (1996) stated that a density of 8 snails/m² (32,376 snails/acre) could reduce rice yields by 90%, and snail densities in our experiment bracket that of Naylor (12 snails/m² = 46,729/acre in Study 1 and 7 snails/m² = 28,037/acre in Study 2). Snails were sorted by weight and then randomly allocated to each tank so that all treatment tanks had similar amounts of snail biomass (i.e., mean weights of 658.7 ± 9.2 g and 407.7 ± 7.1 g in Studies 1 and 2, respectively). Shell height of snails used in these experiments ranged from 58 to 74 mm, and biomass per snail ranged from 50 to 86 g.

Eight circular fiberglass tanks (inside diameter 105 cm, water depth 55 cm) were used in this experiment with 4 pots of each macrophyte species placed in a completely randomized design in each tank. Four tanks were used as controls and contained only macrophytes, while the remaining four tanks were populated with macrophytes and *P. insularium*. All tanks were covered with fiberglass insect screening to ensure containment of the snails in treatment tanks and to maintain consistent light conditions between snail tanks and control tanks. Feeding preference data were collected every other day (Study 1) or every third day (Study 2). One pot of each macrophyte species was randomly removed from each tank at each data collection interval, resulting in four replicates of each treatment (control vs. snails). This allowed us to account for macrophyte growth during the course of the each study. Two replicates of this experiment were conducted in Fall 2005. Study 1 ran from 22 Sept. to 30 Sept. and Study 2 ran from 24 Oct. to 2 Nov. Experimental parameters were similar in both studies except for snail density (10 snails per tank in Study 1 and 6 snails per tank in Study 2) and macrophyte removal interval (2, 4, 6 and 8 d in Study 1 and 3, 6, 9 and 12 d in Study 2). Snails consumed macrophytes more quickly than anticipated in Study 1, so snail density and macrophyte removal interval for Study 2 were modified in an attempt to more clearly identify the snails' preference among the macrophytes offered. Separate analyses were performed for each study to

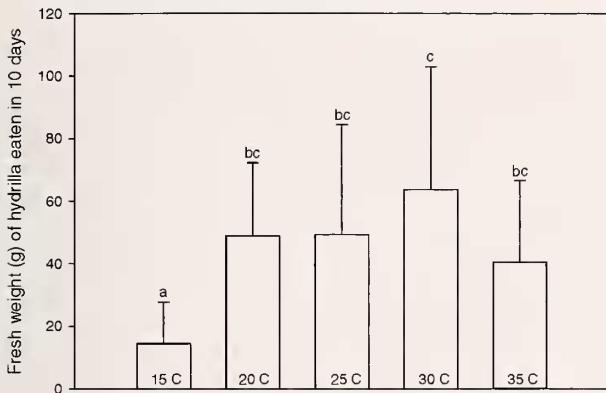


Figure 1. Amount of *H. verticillata* eaten by *P. insularum* under various temperature regimes. Each bar represents the mean of four replicates (snails) per temperature regime and temperature regimes coded with the same letter indicates that *H. verticillata* consumption was not significantly different at $P = 0.05$.

account for seasonal differences in plant growth. Each study was treated as a factorial ($2 \times 7 \times 4$) design, with 2 treatments (snails vs. control), 7 macrophyte species and 4 macrophyte removal intervals. Macrophyte shoot material was weighed to determine fresh weights for all treatments and percent macrophyte material eaten by snails was then calculated by comparing uneaten macrophyte weight of each species in snail tanks to the mean of the same macrophyte species in control tanks. Direct consumption data were not analyzed because macrophyte biomass varied by species (e.g., three rooted plantlets of *V. americana* weigh considerably more than ten 10-cm-long apical cuttings of *Chara* sp.), so the use of percentage data allowed us to standardize consumption across macrophytes of disparate biomass. These percentage data were subjected to analyses of variance (SAS Version 9.1, SAS Institute Inc., Cary, NC, USA) to detect differences between treated and control plants of the same species and differences among plant species harvested at a given time interval.

RESULTS

Effect of Temperature on Herbivory

Snails consumed less plant material at 15°C than at intermediate and high temperatures (20°C, 25°C, 30°C and 35°C) (Figure 1). Also, snails grew faster at intermediate temperatures (20°C, 25°C and 30°C) than at low and high temperatures (15°C and 35°C) (Figure 2). Snails held at 30°C consumed an average of 63.8 g of *H. verticillata* over the course of the study (a daily average of 10.0 g of *H. verticillata* per kg of snail weight) (Figure 1) and gained an average of 2.3 g of biomass over the course of the 10-day study period

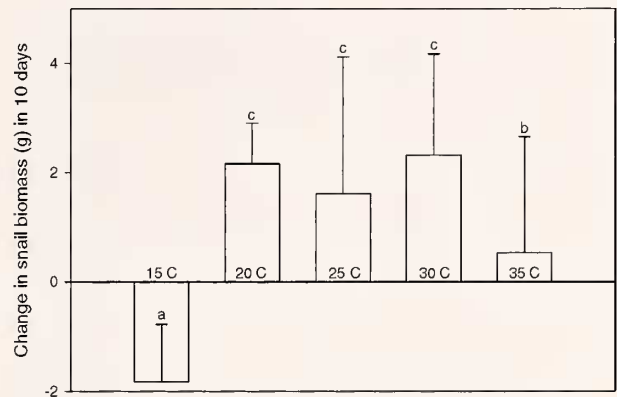


Figure 2. Change in biomass of *P. insularum* under various temperature regimes. Each bar represents the mean of four replicates (snails) per temperature regime and temperature regimes coded with the same letter are not significantly different at $P = 0.05$.

(Figure 2). In contrast, snails kept at 15°C ate an average of 14.5 g of *H. verticillata* during the course of the study (a daily average of 2.3 g of *H. verticillata* per kg of snail biomass) (Figure 1) and actually lost an average of 1.8 g of body weight during the 10-day study period (Figure 2). These results indicate that optimum consumption of the submerged plant *H. verticillata* by *P. insularum* occurred over a wide temperature range (20 to 35°C). However, snail growth was greatest at temperatures of 20 to 30°C.

Feeding Preference

Snail weight did not change significantly during the course of Study 1, as final mean biomass per tank was 655.8 ± 5.7 g. Snails in Study 1 preferred *N. guadalupensis*, *Chara* sp. and *H. verticillata* to *P. illinoensis*, *V. americana*, *M. aquaticum* and *E. densa*; with no difference noted among *N. guadalupensis*, *Chara* sp. and *H. verticillata* at any sampling interval (Figure 3a). Snails ate 89.5%, 82.4% and 75.2% of *N. guadalupensis*, *Chara* sp. and *H. verticillata*, respectively, within two days of commencement of the study and had consumed 100% of these species by the fourth day of Study 1 (Figure 3a). Snails selected *P. illinoensis* and *V. americana* over *M. aquaticum* and *E. densa* when most-preferred macrophytes were depleted. Snails consumed *M. aquaticum* when most-preferred and less-preferred macrophyte species were depleted, but typically fed on leaves and not stem material. Fresh biomass of *E. densa* in snail tanks was not different from that in control tanks at the conclusion of the study; therefore, *E. densa* was not eaten by snails, even when all other plant material had been consumed. Most-preferred macrophytes in Study 1 were *N. guadalupensis*, *Chara* sp. and *H. verticillata*. Less-preferred macrophytes *P. illinoensis* and *V. americana*

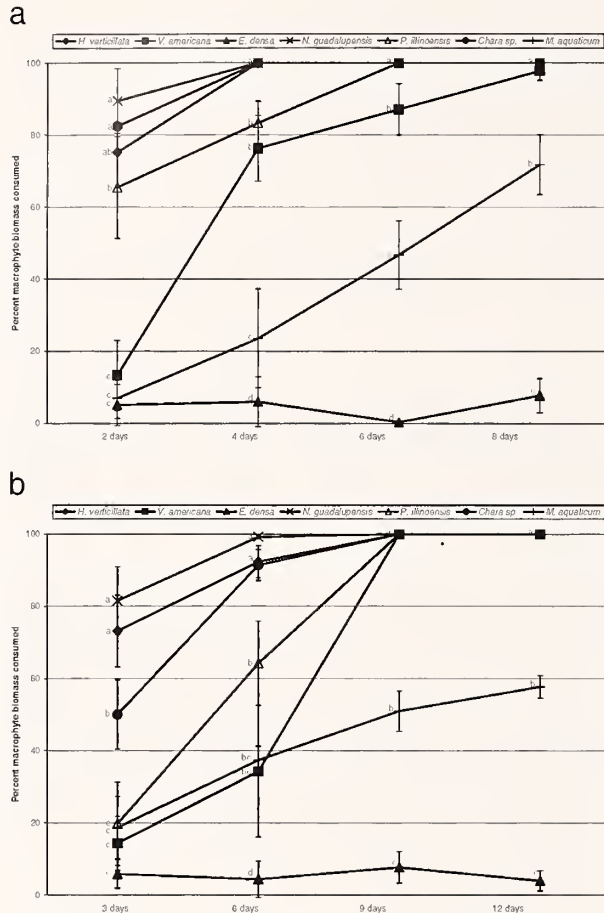


Figure 3a. Percent macrophyte biomass eaten by *P. insularum* during Study 1. Each point represents the mean of four replicates per species and species coded with the same letter are not significantly different at $P = 0.05$. Error bars indicate standard error.

Figure 3b. Percent macrophyte biomass eaten by *P. insularum* during Study 2. Each point represents the mean of four replicates per species and species coded with the same letter are not significantly different at $P = 0.05$. Error bars indicate standard error.

were consumed when most-preferred macrophytes were depleted, and least-preferred macrophytes (with little or no feeding damage) were *M. aquaticum* and *E. densa*.

Snail weight did not change significantly during Study 2, as final mean biomass per tank was 410.3 ± 8.0 g. Snails in Study 2 preferred *N. guadalupensis* and *H. verticillata* to *Chara sp.*, *P. illinoensis*, *V. americana*, *M. aquaticum* and *E. densa*, with no difference noted between *N. guadalupensis* and *H. verticillata* at any sampling interval (Figure 3b). Snails ate 81.5% and 73.2% of the *N. guadalupensis* and *H. verticillata*, respectively, within three days of commencement of the study. Snails preferred *Chara sp.* to *P. illinoensis*, *V. americana*, *M. aquaticum* and *E. densa* and consumed 50.0% of *Chara sp.* by the third day of Study 2

(Figure 3b). There was no difference in consumption of *N. guadalupensis*, *H. verticillata* and *Chara sp.* by the sixth day of Study 2 because nearly all macrophyte material of these most-preferred species was consumed prior to day 6 (Figure 3b). Snails selected *P. illinoensis* over *V. americana*, *M. aquaticum* and *E. densa* when most-preferred macrophytes were depleted and consumed *V. americana* in preference to *M. aquaticum* and *E. densa* when most-preferred macrophytes and *P. illinoensis* were scarce. As in Study 1, snails fed on leaves of *M. aquaticum* when preferred species were scarce and *E. densa* was not eaten by snails even when all other macrophyte material had been consumed. Most-preferred macrophytes in Study 2 were *N. guadalupensis* and *H. verticillata*. The less-preferred macrophyte *Chara sp.* was selected over *P. illinoensis* and *V. americana*, and least-preferred macrophytes (with little or no feeding damage) were *M. aquaticum* and *E. densa*.

DISCUSSION

This research revealed that *P. insularum* consumed the greatest amount of macrophyte biomass and accumulated the greatest amount of body weight when exposed to moderate temperatures (i.e., 20°C to 30°C). This finding does not bode well for Florida's wetlands and waterways, since water temperature falls in this range throughout most of the year in central and southern Florida. These results also showed that *P. insularum* does indeed exhibit a feeding preference if offered an assortment of submerged macrophytes over a short time interval. However, it is unlikely that macrophyte origin plays a role in *P. insularum*'s food selection, since both native (*N. guadalupensis*) and exotic (*H. verticillata*) species were preferred in both studies. Three macrophyte species (including the weed *H. verticillata*) were most preferred, while *E. densa* was completely rejected by snails in this experiment, even when the majority of other macrophyte material had been consumed. It is interesting to note that *H. verticillata* (native to Africa or Asia and strongly preferred by *P. insularum*) and *E. densa* (native to South America and rejected by *P. insularum*) are both members of the Hydrocharitaceae, as is *Elodea canadensis* LC Rich. in Michx (common waterweed). Other researchers (e.g., Carlsson and Lacoursiere, 2005; Estebenet, 1995) have noted that *P. canaliculata* will not eat *E. canadensis*, which is native to temperate regions of North America; in fact, snails offered only *E. canadensis* by Estebenet (1995) refused to eat the macrophyte and eventually starved to death. These three species are submerged macrophytes that are morphologically similar and difficult to distinguish from one another, so the reason for the snails' preference for *H. verticillata* and rejection of *E. densa* and *E. canadensis* is unclear.

It is commonly thought that macrophytes employ structural defenses (e.g., spines, thorns or toughness) to deter feeding by herbivores. Pennings and Paul (1992) found that plant toughness and calcification deterred feeding by the marine gastropod *Dolabella auricularia* (Lightfoot, 1786) (sea-hare). However, *D. auricularia* is able to sequester plant secondary metabolites that may act as chemical feeding deterrents in other herbivorous species. Chemical defenses against herbivory have been extensively studied in terrestrial plants but have only recently gained attention in aquatic macrophytes. Secondary metabolites including alkaloids, glucosinates, polyphenols and flavonols have been identified in a number of aquatic macrophytes and reduce or prevent consumption by herbivores. Erhard et al. (2007) found that flavonoids and other allelochemicals produced by *Elodea nuttallii* (Planch.) St. John (western waterweed) reduced feeding by the larvae of the generalist pyralid aquatic moth *Acentria ephemerella* (Lepidoptera, Pyralidae). Herbivory by *Procambarus clarkii* (Girard, 1852) (red swamp crayfish) was depressed in *Habenaria repens* Nutt. (aquatic orchid) by an endogenous ester (Wilson et al., 1999) and in *Saururus cernuus* L. (lizards-tail) by an array of lignoid metabolites (Kubanek et al., 2001). *Rorippa nasturtium-aquaticum* (L.) Hayek (syn. *Nasturtium officinale*) (watercress) is protected by 2-phenylethyl isothiocyanate, a chemical synthesized by the endogenous glucosinolate-myrosinase system and highly toxic to freshwater gastropods in the genus *Physella* (Kerfoot et al., 1998; Newman et al., 1992). It is unknown whether *E. densa* used in our experiment utilizes chemical defenses such as these to prevent or reduce herbivory; however, the leaf structure and morphology of *E. densa* (rejected by *P. insularum*) are similar to that of the closely related and most-preferred *H. verticillata*, so it is unlikely that structural defenses were responsible for *P. insularum*'s rejection of *E. densa*. It is possible that *E. densa* possesses a chemically based feeding deterrent system to deter herbivory by *P. insularum*. While this question is beyond the scope of our experiment, it certainly merits further investigation.

The majority of studies investigating the impact of herbivory by species of *Pomacea* have focused on *P. canaliculata* (channeled apple snail), the type species for the "canaliculata complex" of which *P. insularum* is a member. Cazzaniga (2002) suggested that any *canaliculata*-like apple snail had the potential to become a pest and cause damage to aquatic ecosystems, so it is likely that the field behavior of *P. insularum* will be similar to that reported for *P. canaliculata*. Snails belonging to the *canaliculata* complex have been introduced to other parts of the world as biocontrol agents to manage aquatic weeds (Cowie, 2002; Okuma et al., 1994; Wada, 1997). For example, Perera and Walls (1996) found that *P. canaliculata* effectively

controlled *Pistia stratiotes* L. (water lettuce) in the Caribbean. Unfortunately, the snails also feed on native plants, resulting in detrimental effects to the native fauna that rely on endemic plants for food and shelter (Simberloff and Stiling, 1996). Field experiments by Carlsson et al. (2004) revealed that *P. canaliculata* consumed most aquatic vegetation and caused bodies of water to become turbid with a dominance of planktonic algae. These workers also found that densities of >2 snails per m² in some of Thailand's natural wetlands resulted in a shift in ecosystem state and function – virtually all aquatic plants were eaten and serious increases were recorded in nutrient concentrations and phytoplankton biomass (Carlsson et al., 2004). Herbivory by *P. canaliculata* extends to commercially cultivated crops as well; in fact, a density of 8 snails per m² can reduce yields by 90% in *Oryza sativa* L. (rice) (Naylor, 1996). Population densities of *P. insularum*-infested wetlands and flooded agricultural sites are often unavailable, but even small populations can explode quickly since *canaliculata*-type snails are highly fecund (Martin and Estebenet, 2002; Tanaka et al., 1999; Teo, 2004). Based on these reports and the results of our experiments, it is likely that wetland areas infested with *P. insularum* will experience severe damage similar to that reported by Carlsson et al. (2004). Also, drastically reduced yields should be expected in inundated agricultural crops (e.g., *O. sativa*, *Colocasia esculenta* (L.) Schott (taro)) grown in areas like Texas, Louisiana, Florida and Hawaii.

These experiments provide additional documentation regarding the feeding habits of *P. insularum* and the positive influence of moderate temperatures on herbivory and growth of the species. It is unlikely that macrophyte origin plays a role in *P. insularum*'s food selection, so special precautions must be followed to exclude this snail from ecosystems where aquatic macrophytes could be decimated by its presence. Many aquatic fauna rely on submerged vegetation as a habitat for nesting and spawning, so *P. insularum*'s indiscriminate consumption of aquatic macrophytes would have devastating consequences to Florida's ecosystem. Other countries have attempted to use *canaliculata*-type snails to control nuisance aquatic plants, but their indiscriminate feeding habits have eliminated virtually all aquatic vegetation. Most aquatic systems support a variety of herbivores, but these species rarely feed at a level that significantly impacts macrophyte populations. Therefore, it is critically important that *P. insularum* and other *canaliculata*-type snails be excluded or eradicated in Florida and in other states at risk to prevent the decimation of critical aquatic ecosystems. Additional research should be conducted to assess the impact of *P. insularum* on other aquatic macrophytes, including floating, emergent and other submerged species. Of

particular interest would be predictive studies to determine the impact of population density of *P. insularum* on aquatic ecosystems.

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LITERATURE CITED

- BENSON, A. J. 2008. *Pomacea insularum*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL. Revision Date: 8/14/2007. <http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=2599>
- CARLSSON, N. O. L., C. BRONMARK & L. A. HANSSON. 2004. Invading herbivory: The golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology* 85(6): 1575–1580.
- CARLSSON, N. O. L. & J. O. LACOURSIERE. 2005. Herbivory on aquatic vascular plants by the introduced golden apple snail (*Pomacea canaliculata*) in Lao PDR. *Biological Invasions* 7(2):233–241.
- CAZZANIGA, N. J. 2002. Old species and new concepts in the taxonomy of *Pomacea* (Gastropoda: Ampullariidae). *Biocell* 26(1):71–81.
- CAZZANIGA, N. J. & A. L. ESTEBENET. 1984. Revision y notas sobre los habitats alimentarios de los Ampullariidae (Gastropoda). *Historia Naturale* 4:213–224.
- COWIE, R. H. 2002. Apple snails (Ampullariidae) as agricultural pests: their biology, impacts and management. Pp. 145–192 in G. M. Barker (ed.), *Molluscs as Crop Pests*. CABI Publishing: Wallingford.
- DENSON, D. 2005. Channeled apple snails invade numerous Florida waters. Florida Department of Environmental Protection, Tallahassee, FL. <http://www.leoncountyfl.gov/lcswm/PomaceaCanaliculata.pdf>.
- ERHARD, D., G. POHNERT & E. M. GROSS. 2007. Chemical defense in *Elodea nuttallii* reduces feeding and growth of aquatic herbivorous *Lepidoptera*. *Journal of Chemical Ecology* 33:1646–1661.
- ESTEBENET, A. L. 1995. Food and feeding in *Pomacea canaliculata* (Gastropoda:Ampullariidae). *Veliger* 38(4): 277–283.
- ESTEBENET, A. L. & N. J. CAZZANIGA. 1992. Growth and demography of *Pomacea canaliculata* (Gastropoda: Ampullariidae) under laboratory conditions. *Malacological Review* 25:1–12.
- ESTEBENET, A. L. & P. R. MARTIN. 2002. *Pomacea canaliculata* (Gastropoda: Ampullariidae): life-history traits and their plasticity. *Biocell* 26(1):83–89.
- FUKUSHIMA, Y., S. NAKAMURA & N. FUJIYOSHI. 2001. Preference and feeding of apple snail (*Pomacea canaliculata*), for fruits and vegetables. *Japanese Journal of Crop Science* 70(3):432–436.
- FLMNH. 2007. Florida Museum of Natural History – University of Florida Invertebrate Zoology Main Collection. <http://www.flmnh.ufl.edu/databases/mala/intro.htm>.
- GETTYS, L. A. & W. T. HALLER. 2007. Apple snails in Florida. *Aquatics* 29(3):4–9. Florida Aquatic Plant Management Society, Inc. Tallahassee, FL.
- KERFOOT, W. C., R. M. NEWMAN & Z. HANSCOM. 1998. Snail reaction to watercress leaf tissues: reinterpretation of a mutualistic ‘alarm’ hypothesis. *Freshwater Biology* 40(2):201–213.
- KUBANEK, J., M. E. HAY, P. J. BROWN, N. LINDQUIST & W. FENICAL. 2001. Lignoid chemical defenses in the freshwater macrophyte *Saururus cernuus*. *Chemoecology* 11:1–8.
- LACH, L., D. K. BRITTON, R. J. RUNDELL & R. H. COWIE. 2000. Food preference and reproductive plasticity in an invasive freshwater snail. *Biological Invasions* 2:279–288.
- MARTIN, P. R. & A. L. ESTEBENET. 2002. Interpopulation variation in life-history traits of *Pomacea canaliculata* (Gastropoda: Ampullariidae) in southwestern Buenos Aires Province, Argentina. *Malacologia* 44:153–163.
- NAYLOR, R. 1996. Invasions in agriculture: assessing the cost of the golden apple snail in Asia. *Ambio* 25:443–448.
- NEWMAN, R. M., Z. HANSCOM & W. C. KERFOOT. 1992. The watercress glucosinolate-myrosinase system: a feeding deterrent to caddisflies, snails, and amphipods. *Oecologia* 92:1–7.
- OKUMA, M., K. TANAKA & S. SUDO. 1994. Weed control method using apple snail (*Pomacea canaliculata*) in paddy fields. *Weed Research, Japan* 39:114–119.
- PELTZER, P. M. & R. C. LAJMANOVICH. 2003. *Hyla pulchella* predation. *Herpetological Review* 34(3):231.
- PENNINGS, S. C. & V. J. PAUL. 1992. Effect of plant toughness, calcification, and chemistry on herbivory by *Dolabella auricularia*. *Ecology* 73(5):1606–1619.
- PERERA, G. & J. G. WALLS. 1996. Apple snails in the aquarium. TFH Publications Inc: Neptune City, NJ.
- RAWLINGS, T. A., K. A. HAYES, R. H. COWIE & T. M. COLLINS. 2007. The identity, distribution, and impacts of non-native apple snails in the continental United States. *BMC Evolutionary Biology* 7:97. <http://www.biomedcentral.com/1471-2148/7/97>
- SIMBERLOFF, D. & P. STILING. 1996. Risks of species introduced for biological control. *Biological Conservation* 78:185–192.
- TANAKA, K., T. WATANABE, H. HIGUCHI, K. MIYAMOTO, Y. YUSA, T. KIYONAGA, H. KIYOTA, Y. SUZUKI & T. WADA. 1999. Density-dependent growth and reproduction of the apple snail, *Pomacea canaliculata*: a density manipulation experiment in a paddy field. *Research on Population Ecology* 41:253–262.
- TEO, S. S. 2004. Biology of the golden apple snail, *Pomacea canaliculata* (Lamarck, 1822), with emphasis on responses to certain environmental conditions in Sabah, Malaysia. *Molluscan Research* 24(3):139–148.
- THOMPSON, F. G. 1997. *Pomacea canaliculata* (Lamarck, 1822) (Gastropoda, Prosobranchia, Pilidae): a freshwater snail introduced to Florida, U.S.A. *Malacological Review* 30:91.
- WADA, T. 1997. Introduction of the apple snail *Pomacea canaliculata* and its impact on rice agriculture. In: *Proceedings, International Workshop on Biological Invasions of Ecosystems by Pests and Beneficial Organisms*. National Institute of Agro-Environmental Sciences, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Japan.
- WILSON, D. M., W. FENICAL, M. HAY, N. LINDQUIST & R. BOLSER. 1999. Habenariol, a freshwater feeding deterrent from the aquatic orchid *Habenaria repens* (Orchidaceae). *Phytochemistry* 50:1333–1336.